evidence in the Nahuatl vocabulary of the influence of any *tertium quid*. We may positively exclude the supposition of a third, wholly lost and unknown tongue, and unhesitatingly identify the "Alaguilac" of Juarros, with the "Tlacabastleca" of Palacio, and both with the ordinary Nahuatl.*

With this identification the last remaining problem in the aboriginal linguistics of Guatemala is solved. We may now confidently say that there was not a tribe found anywhere on its surface by the first explorers of whose linguistic affiliations we are ignorant. Every one can be assigned to its proper ethnographic group so far as this is practicable by a knowledge of its dialect.

As to the second query, whether this Nahuatl colony immigrated before or after the Conquest, we are without positive evidence. But the letter of Palacio, written in 1576, from observations extending over years previous to that date, indicates distinctly that the language of Acasaguastlan had a recognized and independent existence in his day, and, therefore, that the people who spoke it had been found in place when the Spaniards first mapped out the land.

This colony of Nahuas, which had wandered into the upper valley of the Motagua river, was probably an off-shoot from the extensive settlements which their kindred possessed on the Pacific slope in the present Department of Escuintla, some eighty or ninety English miles distant.

The Classification and Phylogeny of the Artiodactyla. By E. D. Cope.

(*Read before the American Philosophical Society, October 7, 1887.*)

This suborder is well defined, and embraces numerous forms, many of which are living. Although it includes much variety of type, the differences shade into each other so that there is considerable difficulty in expressing the natural system in form. The usual division is into the Omnivora and Ruminantia, which are, in the language of Kowalevsky, the

* The language called the "Apay" mentioned by Palacio as spoken at Acasaguastlan has been identified by Dr. Stoll as the Chorti (*Zur Ethnographie der Rep. Guatemala*, p. 106).

Bunodonta and Selenodonta. The latter names are very expressive of the dental characteristics of the two groups (tubercle and crescent bearing), but not having priority, they have come into use as the adjectives bunodont and selenodont, to describe the types of molar crowns to which they refer. But the divisions themselves can no longer be maintained, in view of the numerous extinct forms now known to connect them. Not only do transitions occur, but they occur at different points. Thus Dichobune is the bunodont which corresponds with the selenodont Cænotherium; and Chœropotamus corresponds in the same way with Hyopotamus, Anthracotherium standing between. If it be desirable to name the natural groups into which the families fall, names enough exist in works on the subject, but the divisions they have been applied to are not exactly in accordance with the present writer's views of their true relations. These are presented in the following table. In this work I have been much aided by the Papers of Turner and Flower, which appeared in the Proceedings of the Zoölogical Society, of London, for 1850 and 1875; and of Gill in Smithsonian Miscell. Collec. 1873.

Before presenting the tables and phylogenetic diagrams, the author wishes to make an explanation. Statements as to the phylogeny of a given group, as family, or genus, are intended to apply to them *as defined in the present paper in the tables;* in other words, the phylogenies represent the history of particular structures. There is a tendency among writers, even with some of the best, in considering questions of phylogeny, to restrict their attention to some particular species of a genus, or genus of a family, and to consider all the minor peculiarities of said species or genus, whether appropriate to the wider question before them or not. In brief, I have not attempted to present any phylogeny of species. It will be long before we have the necessary material for that.

I. Superior molars tritubercular (Pantolestoïdea).

Molars bunodont; four digits.....*Pantolestidæ.*

II. Superior molars quadritubercular with an intermediate fifth.

1. Three digits (Anoplotheroïdea).

Intermediate tubercle anterior.....*Anoplotheriidæ.*

11. Two or four digits (Anthracotheroïdea).

A. The intermediate tubercle posterior.

Four digits; molars bunodont.....*Dichobunidæ.*

Four digits; molars selenodont.....*Cænotheriidæ.*

AA. The intermediate tubercle anterior.

Four digits; one series of V's below.....*Anthracotheriidæ.*

Two or four digits; two series of V's below.....*Xiphodontidæ.*

III. Superior molars quadritubercular, without an intermediate fifth.

A. Molars bunodont (Suoïdea).

Four digits.....*Suidæ.*

Two digits.....*Elotheriidæ.*

AA. Molars with cross-crests (Listriodontoïdea).

Premolars different from molars.....*Listriodontidæ*.

AAA. Molars selenodont (with four crescents above).

a. Inferior molars with one series of crescents (Merycopotamoïdea).

Premolars unlike molars.....*Merycopotamidæ*.

aa. Inferior molars with two series of crescents.

β. Superior premolars (except premolar four) with one crest (Cameloïdea).

γ. "Fourth premolar like molars below, with three crests above."

Two digits only (four? in Agriochœrus).....*Dichodontidæ*.

$\gamma\gamma$. Fourth premolar entirely different from molars.

δ. Navicular and cuboid bones distinct from each other.

ε. Superior incisors present.

No cannon bone; a vertebrarterial canal.....*Oreodontidæ*.

No vertebrarterial canal; no cannon bone.....*Poëbrotheriidæ*.

No vertebrarterial canal; a cannon bone.....*Protolabididæ*.

$\varepsilon\varepsilon$. No superior incisors (except incisor three).

No vertebrarterial canal; a cannon bone; superior p. m. iv with external and internal crests.....*Camelidæ*.

Like Camelidæ, but superior p. m. iv a simple cone.....*Eschatiidæ*.

$\delta\delta$. Navicular and cuboid bones coössified.

All premolars but No. iv without internal crescent.....*Tragulidæ*.

$\beta\beta$. Superior premolars 2–3–4 with internal as well as external crest; a naviculocuboid bone; no superior incisors (Boöidea).

Superior p. m. ii without internal crescent.....*Moschidæ*.

Superior p. m. ii with internal crescent.

Horns permanent, originating distinct from skull.....*Giraffidæ*.

Horns permanent, processes of the skull.....*Bovidæ*.

Horns periodically shed.....*Cervidæ*.

Of the preceding sixteen families, ten are extinct. The six families with living representatives are the Suidæ, the Tragulidæ, the Camelidæ, the Moschidæ, the Cervidæ, the Giraffidæ and the Bovidæ.* Thus none of the primary divisions, I and II, have recent representatives. But few of them in fact (some Cænotheriidæ and Anthracotheriidæ) survived the Eocene epoch. Division III is, on the other hand, characteristic of Miocene and recent time, except that some specimens of Gelocus of the Tragulidæ have been found in Upper Eocene beds. Several genera of Tragulidæ,

*Antilocapra is sometimes separated from the Bovidæ as the type of a family, because it is said to sometimes shed its horny horn-sheath. This character, were it really normal, has no significance sufficient for the establishment of a family division.

with Elotherium and Poëbrotherium and Oreodon, belong to Oligocene beds.

Tubercular or bunodont molars are of prior age to selenodont molars, phylogenetically speaking. Of the former, the tritubercular type, it has already been shown, is ancestral to the quadritubercular type. Pantolestidæ are then clearly ancestral to all known Artiodactyla, and are themselves probably the descendants of the lost Amblypoda Hyodonta, whose existence I have anticipated on hypothetical grounds. Of the remaining families which are constructed on the quadritubercular basis, there are two types, as represented in divisions II and III of the preceding table. The intermediate or fifth lobe is especially characteristic of Eocene Artiodactyla. The intermediate tubercles exist in the Pantolestidæ, and one of them is preserved in the families of division II; but in group *A* it is the posterior one, and in group *AA* it is the anterior one. In the Suidæ and Elotheriidæ, which are permanently bunodont, the intermediates are either lost or so divided as to lose their distinctive character. In Elotherium traces of both the intermediates are visible, but they are obscure. The genetic relations of the families with five lobes to those with four are supposed by Schlosser to be direct and ancestral. This looks probable in the case of the Merycopotamidæ of the latter group, which has inferior molars like those of Hyopotamus of the former group. Whether the remaining families of division III *AAA* (see table) (four-lobed) came off from the families of division II (five-lobed) is uncertain. It is probable that the fifth and sixth (or intermediate) tubercles were present in all primitive Artiodactyla, but they may have been lost, as in the Suidæ, in the bunodont stage, which gave origin to III *AAA*, so as to be wanting from the earliest four-lobed selenodont ancestors. Of the two types of II, the division *A* (Dichobunoïdea) is supposed by Schlosser to have been the ancestor of the true selenodonts (III *AAA*), but excepting in the case of Merycopotamidæ this has not yet been demonstrated. Scott suspects with reason that the quinquetubercular Protoreodon is the ancestor of the quadritubercular Oreodon.

Leaving this debatable question, I refer to the family of the Anoplotheriidæ. The remarkable structure of the feet discovered by Gervais, and shown by Schlosser to belong to this family, distinguishes it at once from all families of this and all other orders.

The second digit is well developed in both feet, and stands inwards at a strong angle to the other toes. A rudimental fifth is present in the manus, but not in the pes. The latter is therefore tridactyle. The third and fourth digits are equal in the pes, but the third exceeds the fourth in the manus, giving an entirely perissodactyle character. Some didactyle forms have been placed in this family, but this is inadmissible on ordinary taxonomic principles. The divergent inner toe is supposed to have supported a web, useful in an aquatic life. As remarked by Schlosser, the origin of the Anoplotheridæ is entirely obscure as yet, the only ancestor yet known being the Pantolestidæ. It is probable that some

unknown member of the Anthracotheroidea, which had bunodont teeth, may form one of the missing links. Cebochœrus offers the proper type of dentition, and the number of toes (four, Schlosser) is also appropriate, but whether there are any structural obstacles to its being ancestral to the Anoplotheriidæ I do not know.

Anthracotheriidæ can be properly supposed to have descended from a type of Pantolestidæ with well-developed lateral toes, by the addition of the fourth tubercle, and the loss of the posterior intermediate; while the Dichobunidæ have had the same origin, the posterior intermediate cusp being preserved. The Xiphodontidæ may be supposed to have come off from the Anthracotheriidæ by the usual process of diminishing the lateral digits and developing both sets of crescents in both superior and inferior molars. This family carried the specialization of the five tubercled type farther than any other.

The Suoïdea have come off from the Pantolestoïdea by the addition of the fourth (posterior internal) tubercle to the superior molars. Some genus with better developed lateral (second and fifth) digits than Pantolestes must have been the ancestor. Such a form will be discovered. It has been already anticipated by Schlosser.*

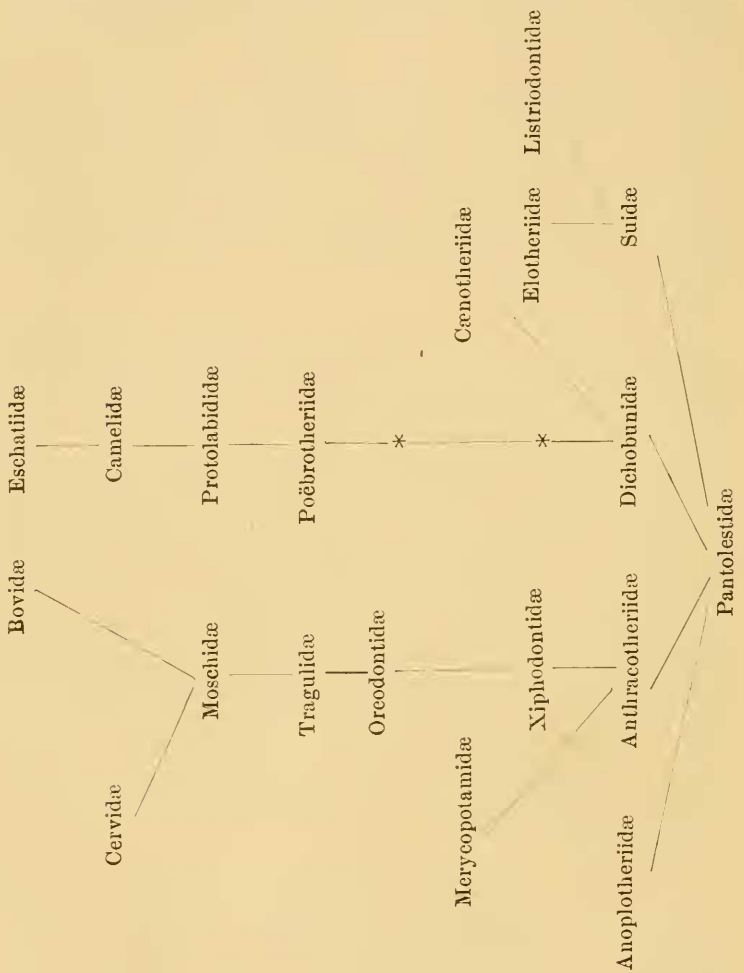
It is evident that the Listriodontidæ form a special short side-branch, with a type of molar teeth, especially in the lower series, resembling some of the Perissodactyla. The nearest approach to it is seen in the genus Platygonus of the Suidæ, which has more complex premolars. Here the four cusps of the quadritubercular bunodont type are fused together into transverse crests. The limbs of Listriodon are unknown.

It is a circumstance confirmatory of the view that the Cameloïdea and Boöïdea are descendants of the Anthracotheroïdea rather than of the Suoïdea, that no genus of the latter superfamily shows the least tendency to assume a selenodont structure of the molars. It is therefore not unlikely that the two groups named may have had the history of the Merycopotamoïdea already referred to. They did not probably come from the Merycopotamoïdea themselves, since the geological age of the latter is too late. Of course, however, members of this group may be yet discovered in earlier formations.

The problems of the phylogeny of the remaining groups are less difficult, and have been largely solved by the investigations of Kowalevsky and Schlosser. Tragulidæ have been derived from Oreodontidæ with simpler premolar teeth than the typical forms, (*e. g.* Dorcatherium and Lophiomeryx). In turn they have given origin to primitive Bovidæ (Cosoryx) through Gelocus, which have then branched off into specialized Bovidæ on the one hand, and Cervidæ on the other. The Poëbrotheriidæ have originated from some family with diminished lateral digits, perhaps the Dichobunidæ, various intermediate genera being yet unknown. They

* Morphologisches Jahrbuch, 1886, p. 77.

are the direct ancestors of the Protolabididæ, the camels, and the Eschatiidæ. These relations may be expressed in the following table:



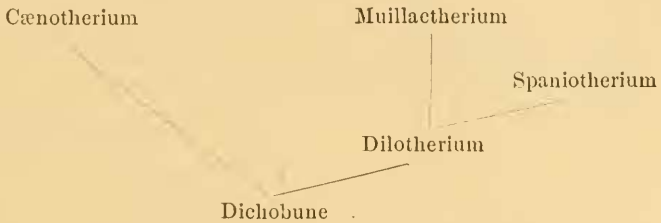
Of PANTOLESTIDÆ but one genus is known. The premolars are all simple in the upper jaw, except the fourth, which has one external and one internal tubercle.

The structure of the premolars in Anoplotherium is complex for so primitive a type, and the third superior has an internal crest as well developed as in some of the Boöidea. To the ANOPLOTHERIIDÆ are referred, besides Anoplotherium, Diplobune of Fraas and Dacrytherium, Mixto-

therium and Mixochœrus of Filhol. But the structure of the feet of the latter genera is unknown. In Mixtotherium the fourth premolar is more, and the others less complex than in Anoplotherium.

The known genera of DICHOBUNIDÆ are Dichobune of Cuvier, with Spaniotherium and Dilotherium of Filhol, in which the intermediate tubercles are less developed than in Dichobune. They are related to the two selenodont genera of CÆNOTHERIIDÆ, Cænotherium and Muillactherium. The latter differs from the former in the absence of the intermediate crescent from the last superior molars. The species of Cænotherium differ in the absence or presence of a short diastema in the dental series, and in its position in the lower jaw, whether behind the first or second premolar.

The Dichobunid bunodont genera are ancestral to the Cænotheriid selenodont genera in the following fashion :

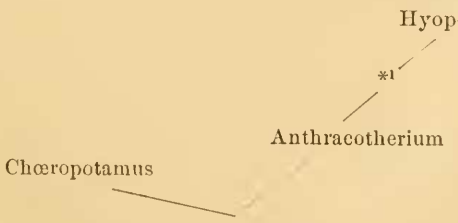


This family terminated with the selenodont genera, which, as Schlosser remarks, left no known descendants.

The ANTHRACOTHERIIDÆ present but few variations. Four genera are known, which differ as follows :

Entirely bunodont ; no diastemata ; canines developed. *Cebochœrus* Gerv.
Cusps of superior molars little flattened ; diastemata ; canines large *Chœropotamus* Cuv.
Cusps of superior molars flattened ; no diastemata ; canines large *Anthracotherium* Cuv.
Cusps of superior molars crescentoid in section ; diastemata ; canines large in males..... *Hyopotamus* Owen.

The three genera last named cannot, as Schlosser remarks, be related in direct lines, but through common ancestors ; as may be shown thus :



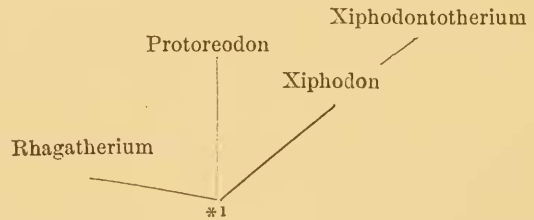
The ancestral genus is bunodont, without diastemata, and with well-developed canines. The hypothetical genus (1) is selenodont, with short diastema, and well-developed canines.

The certainly known genera of the XIPHODONTIDÆ are four, which differ as follows:

Molars bunodont; diastemata; canines large.....*Rhagatherium* Pict.
Molars selenodont; diastemata; canines medium.*Xiphodontotherium* Filh.
Molars selenodont; no diastemata; canines not distinct in form
Xiphodon Cuv.
Molars selenodont; no diastemata; superior canine developed; inferior p. m. 1 functioning as canine.....*Protoreodon* S. & O.

Cryptomeryx Schl. probably belongs here.

The relations of these genera are clearly somewhat like those of the preceding family. The bunodont condition of the molars of Rhagatherium is primitive, while its diastemata are the reverse. The continuous dental series of Xiphodon is primitive, while the detailed structure of the molars is advanced. These relations may be thus shown:



The hypothetical genus 1 is simply a bunodont without diastemata, and with well-developed canines.

The pigs, SUIDÆ, are an old family, although no genus is known prior to Miocene time. The genera present considerable variety among themselves, but some of the existing genera differ very little from some of the earliest. The greatest diversity is seen in the modifications of the incisor and canine teeth. The following represents the characters:

I. Metapodials fused proximally (Dicotylinæ).

a. Premolars like molars.

Premolars $\frac{3}{3}$; cusps of molars separate.....*Dicotyles* Cuv.
Premolars $\frac{3}{3}$; cusps of molars united into partial cross-crests
Platygonus Lec.

II. Metapodials distinct (in some unknown); molars without cementum; incisors normal (Suinæ).

a. Fourth premolar with one external tubercle.

Four superior premolars.....*Thinohyus* Marsh.
Three superior premolars ... .*Chœnohyus* Cope.

aa. Fourth superior premolar with two external tubercles.

β. Superior canines decurved.

Superior canines small.....*Hyotherium* Von Myer.

$\beta\beta$. Superior canines recurved.

Molars with four much plicate tubercles on each..*Hippohyus* Cautl. Falc.

Molars with numerous irregular accessory lobes; premolars $\frac{4}{4}$..*Sus* Linn.

No accessory lobes; premolars $\frac{3}{2}$.....*Babirussa* Cuv.

III. Metapodials distinct; superior incisors reduced in number; molars reduced in number, and the valleys filled with cement (Phacochœrinæ).

Superior incisors one; premolars none; molars $\frac{3}{2}$, with numerous tubercles; superior canines recurved.....*Phacochœrus* Cuv.

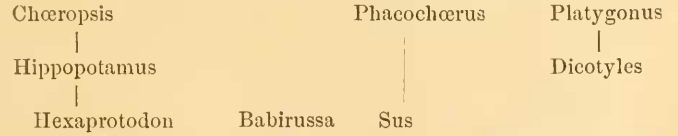
IV. Metapodials distinct, distally keeled behind only; inferior incisors straight, subcylindric (Hippopotaminæ).

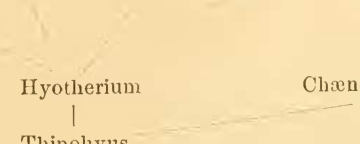
Six lower incisors; orbit closed.....*Hexaprotodon* Caut. Falc.

Four lower incisors; orbit closed.....*Hippopotamus* Linn.

Two lower incisors; orbit not closed.....*Chœropsis* Leidy.

The absence of intermediate types renders the determination of the phylogeny of the genera as yet impracticable. The main features may however be foreshadowed. The most generalized form is Thinohyus, since its dentition is in all respects the most simple, while it preserves the full number of teeth. It may readily have given origin to the Dicotyline line on the one side, and Sus and its immediate allies on the other. Babirussa is another derivative from the same center. Phacochœrus may have come from some ally of Sus, since it carries to a great extreme the peculiarities of the latter genus. The ancestry of Hippopotamus is less easily determined. Its imperfect distal metapodial keels, which only exist on the posterior face of the condyle, bespeak for it an ancient ancestor. Its molar type is merely a complication of the quadritubercular, while the characters of its canines are an exaggeration of those of the primitive forms already mentioned. Several other genera, as Dicotyles and Sus, display the decumbent incisors which prepare the way for the remarkable straight digging incisors of Hippopotamus. The genus Chœropsis eases the passage backwards. These relations may be expressed as follows:





But one genus of ELOTHERIIDÆ is known. The character of the feet, reduced to but two metapodials in a bunodont genus of the Lower Miocene or Oligocene, surprised Kowalevsky, who first determined the fact, and has excited similar feelings in other naturalists. But the precocious diminution of the lateral digits has been already observed in various primitive genera, as Pantolestes and Dichobune, and from one or perhaps both of these forms Elotherium was derived. In its dental characters it is of the simple suilline type. The type early ceased to exist, its latest forms being American, and some of them rivaled the rhinoceroses in dimensions.

The LISTRIODONTIDÆ and MERYCOPOTAMIDÆ include but one genus each, though others probably will be discovered. I therefore turn to the OREODONTIDÆ which embraces a larger number of forms. Its characters are as follows:

Dentition: superior incisors present; molars selenodont. Cervicals with the transverse processes perforated by the vertebrarterial canal. No alisphenoid canal. Ulna and radius, and tibia and fibula distinct. Metapodial bones four on each foot, with incomplete distal trochlear keels. Lunar bone not supported by magnum. Navicular and cuboid bones distinct. The details of the structure express various affinities. The axis is intermediate between that of the suilline and ruminant Artiodactyla; the other cervicals are suilline, while the remaining vertebræ are ruminant. The scapula is ruminant, not suilline; while the humerus is like Anoplotherium. The radiocarpal articulation is intermediate between that of hogs and ruminants. The unciform supports the lunar bone. The sacrum is ruminant, the ilium suilline. The femur and tarsus are much like those of the peccary.

The known genera of this family are the following:

A. Orbit complete; premolars four, the fourth with one external crescent. First premolar below functioning as canine.

a. No facial vacuities.

Premaxillaries distinct; otic bullæ not inflated; five digits in manus *Oreodon* Leidy.

Premaxillaries distinct; otic bullæ inflated; four digits in manus *Eucrotaphus* Leidy.

Premaxillaries coössified; otic bullæ inflated..... *Merycochœrus* Leidy.

aa. Facial vacuities present.

Premaxillaries coössified, dentigerous; vacuities prelachrymal only *Merychyus* Leidy.

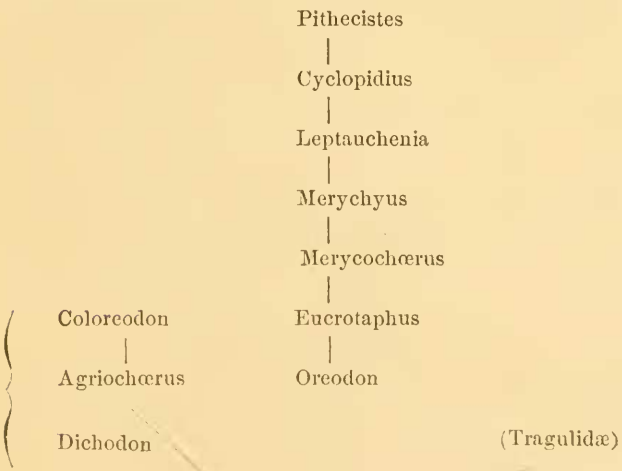
Incisors six above, persistent; vacuities prelachrymal and prefrontal; nasal bones much reduced..... *Leptauchenia* Leidy.

Incisors very few, caducous; vacuities very large..... *Cyclopidius* Cope.

AA. Inferior premolars three. True inferior canine functional.

Inferior incisors one on each side..... *Pithecistes* Cope.

Starting from Oreodon as the ancestral form, Eucrotaphus follows at a little distance. The presence of the pollex observed by Scott in Oreodon proves that it must be referred to a five-toed common ancestor with Dorcatherium. The enlarged bullæ are added in Eucrotaphus, and the coössified premaxillaries in Merycochœrus and Merychyus. The latter commences the facial vacuities, which reach such huge proportions in Leptauchenia and Cyclopidius. The loss of the incisor teeth from both jaws, and diminished size, indicate that decadence is going on in Cyclopidius, but the last term is reached in Pithecistes. Here not only incisors but a premolar disappears. This family, once powerful in numbers, size and strength, disappeared with the Upper Miocene period in North America. These relations may be thus displayed. A common ancestor with Dorcatherium is assumed. This will be a genus like Protoreodon S. & O., but without the caniniform inferior p. m. i of that genus, and probably with the fifth crescent of the superior molars. Agriochœrus may have been derived from the same.



*

The geological positions of these genera are as follows :

Oreodontinæ.	No. of Species.	White River Epoch.	John Day Epoch.	Tiheleptus Epoch.	Loup Fork Epoch.
Oreodon Leidy	3	———			
Eucrotaphus Leidy	3	———	———		
Merycochœrus Leidy	8		———	———	
Merychyus Leidy	6			———	———
Leptauchenia Leidy	3			———	
Cyclopidius Cope	2			———	
Pithecistes Cope	3			———	

The Dichodontidæ are allied to the Oreodontidæ and Tragulidæ in the simple form of the premolars, excepting the fourth in both jaws. These resemble, according to Schlosser,* the milk teeth of other ruminants in the genus Dichodon. For the present I associate with this European genus, the American Agriochœrus and Coloreodon, in which the last lower premolar resembles a true molar, and the last upper has two external Vs as in a true molar. The structure of the feet in these genera is unknown, but in Dichodon they are supposed to consist of the two median digits only, which do not form a cannon bone.† It is safe to conclude that the American forms do not possess a cannon bone, and as the presence or absence of lateral digits is not always a family character, I leave them provisionally in the Dichodontidæ to which they are in any case nearly allied. They agree also in the resemblance of the inferior canine to an incisor tooth, but the first premolar is caniniform in the American genera, which it is not in Dichodon. The genera differ as follows :

I. First inferior premolar caniniform.

Premolars three..... *Coloreodon* Cope.

Premolars four..... *Agriochœrus* Leidy.

II. First inferior premolar not caniniform.

Premolars four..... *Dichodon* Owen.

In this instance the genus of more modern type, Dichodon, is the oldest in time (Upper Eocene), the other genera being Lower Miocene. These types have been derived from some common ancestor of the family of Oreodontidæ as here defined. Dichodon may be a descendant of Lophiomeryx, and Agriochœrus be derived from an ancestor in common with that genus and Dorcatherium (for diagram see under Oreodontidæ).

The Tragulidæ has a good many extinct genera, and the genus Tragulus is represented by several living species. It is difficult to separate this family from the Oreodontidæ, and the only character which appears to be

* Beiträge z. Kenntniss d. Stammesgeschichte d. Hufthiere u. Versuch einer System der Paar- u. Unpaarhufer. Morphologisches Jahrbuch, 1886, p. 56.

† The Diplopus of Kowalevsky is supposed to be Dichodon, by Schlosser.

available is the development of a naviculocuboid bone in the posterior foot. If this character be not used, then the two families will form a single natural division. This definition includes in the Tragulidæ the Gelocidæ of Schlosser, a result inevitable on any exact system. The genera remaining, of which the limb structure is known, are defined as below. Several other genera are known from teeth, as Micromeryx, Phaneromeryx, Rutitherium, etc., but since their feet are not described, I am compelled to omit them.

I. Both metatarsals and metacarpals distinct; molars brachyodont (Hypertragulinæ).

a. Lateral toes behind.

Anterior internal crescent of inferior molars represented by a conical cusp.....*Lophiomeryx* Pom.

Interior crescents of inferior molars developed.....*Dorcatherium* Kaup.

aa. No lateral toes behind.

Diastemata in both jaws.....*Hypertragulus* Cope.

II. Metatarsals forming a cannon bone; metacarpals distinct; molars brachyodont (Gelocinæ).

a. Lateral digits of the manus, none of the pes.

Superior premolars with a small internal tubercle.....*Leptomeryx* Leidy.

aa. No lateral digits.

Four lower premolars.....*Gelocus* Aym.

Three lower premolars.....*Bachitherium* Filhol.

III. A metatarsal cannon bone; metacarpals forming a cannon bone; molars brachyodont (Tragulinæ).

a. Lateral digits well developed.

Premolars entirely simple.....*Tragulus* Briss.

aa. Lateral digits weak.

Four inferior premolars, the posterior with branch ridges; superior premolar 3 with strong cingulum.....*Amphitragulus* Pomel.

Three inferior premolars, the posterior with branch ridges; superior premolar 3 with strong cingulum, elongate.*Prodremotherium* Filhol.

IV. Metatarsals and metacarpals unknown; molars hypsodont (Hypisodontinæ).

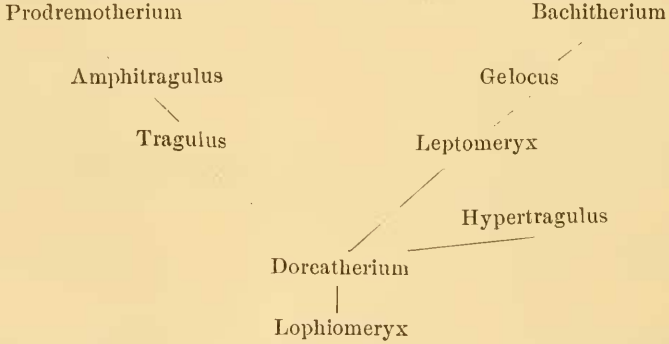
A diastema behind p. m. 2; canines not distinct.....*Hypisodus* Cope.

Of these genera, those with the metatarsals separate, and the simplest premolar teeth, must be the most primitive and nearest the Oreodontidæ.

Dorcatherium, also an existing genus, has four well-developed digits, and is nearest the Oreodontidæ. The only difference between that family and the present one being the presence and absence of the naviculocuboid bone respectively, Dorcatherium must be placed on the Tragulid side of the line. Probably extinct genera will be found which will connect this genus more intimately with the Oreodontidæ, for the slight complication of the premolars of the extinct genera of the latter, testify to earlier members with simpler ones. Lophiomeryx and

Hypertragulus must be associated with Dorcatherium on account of the lack of cannon bone. Lophiomeryx has an inferior type of inferior true molar, and like Dorcatherium has four toes on all the feet. Hypertragulus displays greater specialization in the absence of lateral digits from the posterior feet. The ulna is also coössified with the radius, and there is a naviculocuboid bone. The premolar teeth are nevertheless very simple, and are separated by diastemata in both jaws. It must be regarded as a modified descendant of Dorcatherium on one side of the main line of descent.

In the next group the metatarsals have united while the metacarpals remain separate. This is the case in Leptomeryx of the American Oligocene. In Tragulus the premolars are much simpler than those of the other genera of Section III, and simpler than those of Leptomeryx, so that these two forms must have been derived from an ancestor which combined the simplicity of both forms. For this we must again recur to Dorcatherium, and I therefore insert this genus at the base of the following diagram. With its entirely prismatic molars Hypisodus has one element of superiority, but the number of its superior premolars is unknown.



Of the Poëbrotheriidæ there are two genera. These differ as follows:

First premolar of upper jaw elongate and with two roots
Poëbrotherium Leidy.

First upper premolar short and with a simple conic root
Gomphotherium Cope.

The phylogenetic relations of these genera correspond with their relative geological positions. In Gomphotherium from the John Day (Middle) Miocene, the first premolar is much reduced, probably soon to be aborted, as is the case in later genera of the line, among the Camelidæ. In Poëbrotherium it displays an unusual development, like that of some Tragulidæ.

With the Poëbrotheriidæ we commence a series of families characterized by the absence of the vertebrarterial canal, or the line of the camels proper.

The direct connection with the families previously described is not yet known. The indications point to the Oreodontidæ, but no approach to the cervical vertebræ of the Poëbrotheriidæ has yet been found in that family.

Messrs. Scott and Osborn have described a mammal, from the Bridger Eocene of Wyoming, as a probable member of the camel series, under the name of *Ithygrammodon cameloides*. It is only known from two premaxillary and a part of one maxillary bones. The former are slender and bear a complete set of incisor teeth, which are followed by a large canine. It is probable that this genus belongs in the camel series, but it cannot yet be positively affirmed.

Ancestral to the Camelidæ is the genus Protolabis Cope, which agrees with Procamelus, the earliest genus of that family in most respects, but differs decidedly in having a full set of superior incisor teeth. In this genus we reach the stage, in tracing back the ancestry of the camels, which we find represented by Oreodon, or the Gelocus in the line of the cattle and deer. It is probable, though not certain, that in Protolabis the metapodial bones are combined into a cannon bone as in the Camelidæ. If so it differs materially from its predecessor, the genus Pœbrotherium, and must be regarded as the type of a special family, the PROTOLABIDIDÆ. But one genus of this family is known up to the present time. Its remains occur in the Ticholeptus beds of Oregon and the Loup Fork beds of Nebraska and Kansas.

In the CAMELIDÆ we begin to realize the characters of the latest Artiodactyla, the ruminants. But they differ from the typical forms of these, the Boöidea, in three important points of the osteology, viz., in the absence of a canal of the cervical vertebræ which in other Mammalia encloses the vertebral artery ; the presence of an incisor tooth on each side of the upper jaw ; and thirdly, the incompleteness of the keels of the distal ends of the metapodial bones. This character and that of the presence of incisors, are primitive conditions common to all the early Mammalia. The peculiar cervical vertebræ constitute a specialization, but whether degenerate or progressive remains to be ascertained. In one respect this line exhibits a high specialization, which is present at the earliest known period of its history. This consists in the reduction of the lateral (II and V) metapodial bones, so that but two functional toes remain. This condition has been reached by the more typical artiodactyles after a much longer lapse of time, for most of the extinct and recent types display lateral digits in a well-developed or rudimentary condition ; in but few of them have they totally disappeared. In another respect the line of the camels attains a higher specialization than that of the typical ruminants, although its beginning is that which is common to the entire suborder. This is in the dentition. The reduction in numbers of teeth shown by Owen to characterize the historical succession of all Mammalia, is carried further in the molar series of camels than in any hoofed order ; for in the final term or genus, Eschatius (Cope), there is but one premolar left in the upper jaw, and that is reduced to a simple cone. The true molars never

reach the complexity of those of the other line, of the Bovidæ or oxen, nor do they become prismatic as in that family, but retain the short crown well distinguished from long roots, which belongs to all the earlier Mammalia.

The successional reduction in the numbers of premolar teeth in the family of the Camelidæ is shown in the following table.* There is seen in the genera Protauchenia and Palauchenia a tendency to an increase of complication of the fourth inferior premolar :

I. Premolar teeth $\frac{4}{4}$.

Premolar I separated by diastema.....*Procamelus* Leidy.

II. Premolar teeth $\frac{4}{3}$.

Premolar II below wanting.....*Pliauchenia* Cope.

III. Premolar teeth $\frac{3}{2}$.

Fourth inferior premolar triangular.....*Camelus* Linn.

Fourth inferior premolar composed of two crescents, which enclose a lake (an inferior premolar three?).....*Palauchenia* Owen.

Fourth inferior premolar composed of two crescents, with two posterior tubercles behind them.....*Protauchenia* Branco.

IV. Premolar teeth $\frac{2}{1}$.

Fourth premolar below triangular.....*Auchenia* Illiger.

V. Premolar teeth $\frac{1}{1}$.

Fourth superior premolar composed of two crescents..*Holomeniscus* Cope.

The only genera which include existing species are Camelus and Auchenia, the camels and llamas respectively. It may be remarked that the latter genus, which is confined to the new world, is more specialized than Camelus, which is restricted to the old world.

The succession of these genera in connection with the two preceding families, may be presented as follows :

	No cannon bone.	Cannon bone present.			
	Incisor teeth present.	Incisors one and two wanting.			
	4 premolars.	3 prem's.†	2 prem's.	1 prem'r.	
Lower Miocene	*Gomphotherium*				
Upper Miocene	*Protolabis*	*Procamelus*	*Pliauchenia*		
Pliocene and recent				*Camelus*	*Auchenia*

This table shows that geological time has witnessed, in the history of

* From Proceedings Amer. Philosoph. Soc., 1884, p. 16.

† In lower jaw.

the Camelidæ, the consolidation of the bones of the feet and a great reduction in the numbers of the incisor and premolar teeth. The embryonic history of these parts is as follows: In the fœtal state all the Ruminantia (to which the camels belong) have the cannon bones divided as in Poëbrotherium; they exhibit also incisor teeth, as in that genus and Protolabis. Very young recent camels have the additional premolar of Pliauchenia. They shed this tooth at an early period, but very rarely a camel is found in which the tooth persists. The anterior premolar of the normal Camelus is in like manner found in the young llama (Auchenia), but is shed long before the animal attains maturity. I may add that in some species of Procamelus caducous scales of enamel and dentine in shallow cavities represent the incisor dentition of Protolabis.

In greater detail, the extinct American forms of this line are distributed as follows:

	Eocene.		Miocene.				Pliocene.
	Wasatch.	Bridger	White River.	John Day.	Ticholeptus.	Loup Fork.	Equus.
Pantolestes Cope....	5	1					
Ithygrammodon S. O.		1					
? Stibarus Cope.....			1				
Poëbrotherium Leidy			2				
Gomphotherium Cope				1			
Protolabis Cope.....					1	2	
Procamelus Leidy...						6	
Pliauchenia Cope....						2	
Holmeniscus Cope...							3
Eschatius Cope.....							2

The total number of genera, nine; of species, twenty-six.

The development of the brain displays the same progress that has been shown by Lartet and Marsh to have taken place in other lines of Mammalia. The figures which I have given of the brain, show that while *Procamelus occidentalis* is inferior to the camel in the size and development of the convolutions of the hemispheres, it is in advance of the *Poëbrotherium vilsoni* in these respects.

The development of the camels in North America presents a remarkable parallel to that of the horses. The ancestors of both lines appear together in the Wasatch or lowest Eocene, and the successive forms develop side by side in all the succeeding formations. Camels and horses are standard types in all our Tertiary formations; and they must be learned by any one who wishes to distinguish readily the horizons one from the other. The horse-forms are more numerous in all the beds, in individuals as well as in species. Both lines died out in North America, and of the two, the camels only have certainly held their own in South America. The history of the succession of horses in Europe, although not as complete as that in America, extends over as wide a period of time.

PROC. AMER. PHILOS. SOC. XXIV. 126. 2x. PRINTED DEC. 3, 1887.

Not so with the camels. There is no evidence of the existence of the camel line in the old world prior to the late Miocene epoch; and so far as the existing evidence goes, the new world furnished the camel to the old.

Camelidæ only appear in South American palæontology in the genus Auchenia, in Pliocene time, in the Pampean beds. The best known species are *Auchenia weddellii* and *A. intermedia* of Gervais. It is curious that M. Ameghino, in his report on the fauna of the Miocene age found on the River Parana, which contains the ancestors of so many Pliocene genera, finds none that stand in that relation to the llamas.

The Eschatiidæ includes a single genus represented by large species of North America and Mexico.

We now reach the division of the Artiodactyla, which is especially characteristic of the present period; the Boöïdea, or, as it is sometimes called, the Pecora. It embraces more numerous species than any existing division of the Ungulata, and presents considerable difficulties to the zoölogist who would represent the relations of its contents. As a division it is however well defined by the following peculiarities.

The third and generally the second superior premolar teeth possess an internal crest as well as the fourth. The inferior premolar teeth have oblique transverse crests. The keel of the distal extremity of the metapodial bones extends to the front of the condyle. The lateral metapodials are represented by their extremities only, the middle portion having disappeared. The median pair are united into a cannon bone. There are no superior incisors. The odontoid process of the axis vertebra is trough-shaped. The stomach is divided into three or four parts.

The lowest family of the series is that of the Moschidæ. In its hard parts it differs from the other Bovidæ in the simplicity of the anterior (second) superior premolar, which is without the internal crescent found in the other Boöïdea. In this respect it is intermediate between that division and the Cameloidea, where the fourth premolar only possesses the internal crescent. But two genera of Moschidæ are known, Dremotherium from the Lower Miocene of France, and the living Moschus. Both lack horns and have well-developed canine teeth. The origin of this group is clearly from the Tragulidæ, and the genus of that family which approaches nearest to it is Amphitragulus, which indeed only differs from it in dentition in the imperfection of the internal crest of the third superior premolar. In turn, Dremotherium must be regarded as ancestral to Palæomeryx, the most primitive genus of the Bovidæ.

The Giraffidæ differ (see table of families) in the mode of attachment of the horns. These are originally separate from the skull, but become attached to it like the epiphyses on the extremities of the bones of the skeleton. Their dental characters are like those of the Cervidæ and the lower Bovidæ, the molars being short crowned or brachyodont. It may be that the condition of the horns in Giraffa represents the mode of origin of the horns of the Bovidæ, and that the genus is simply to be reckoned a primitive type in that family. The specialization of the long

neck and fore legs would not exclude it from that family. It is merely an adaptation for the habit of browsing on the foliage of tall trees. In the extinct species of its single genus, Giraffa, these characters are found in a less degree than in the existing one. The most obvious distinction between the Bovidæ and the Cervidæ is in the differing character of the bony processes of the skull, used for offense and defense. But where horns are wanting, as is the case with some genera, these distinctions fall to the ground. The horn-type of the Bovidæ is more primitive than that of the Cervidæ, since the horny process is permanent in the former, and is shed and reproduced annually in the latter. The dental type is, however, never so specialized in the deer, as is the case with the highest genera of Bovidæ, remaining always distinctly rooted, while in Bos and some other genera of the latter they become prismatic. But the lower genera of Bovidæ do not differ from Cervidæ in this respect.

In accordance with these facts the bovine ruminants appear a little before the cervine, though authors generally refer the earliest genera to the latter division. Such are the genera Dicrocerus and Cosoryx,* which appear in the latest Miocene beds. Dicrocerus only differs from Palæomeryx in the possession of horns, which resemble those of deer, but which were, according to Schlosser, never shed, a fact which compels its location in the Bovidæ. In Cosoryx the horns have the same character in this respect, but the teeth are antelopine, or prismatic. It is clearly to be placed in the Bovidæ with Antilocapra (the prong-horn), and it is closely allied to Dicrocerus. Here we see that the point of origin of the two families was from a common ancestor, and that this ancestor was, as has been already expressed by Schlosser, the genus Palæomeryx. Nearly related to this point of departure are the Sivatherium, Bramatherium, and Hydaspidotherium. As they do not shed their horns, they cannot be referred to the Cervidæ. In their covering with the integument, Cosoryx probably possessed a character of Giraffa, which is a primitive stage of the essential character of the horns of the Bovidæ. Perhaps the retention of the primitive dermal character of this investment, instead of its metamorphosis into horn, might be regarded as a basis for a distinct family, the Cosorycidæ. But it is highly improbable that this covering remained in Sivatherium and Bramatherium, whose horns were apparently perfectly naked. It is doubtful whether all these animals can be retained as distinct from the Bovidæ, and I therefore place them in two subfamilies of that family. The Cosorycinæ, which will include Cosoryx and Blastomeryx, are characterized by the sheath of the horns being dermal; the Sivatheriinæ by the absence of any sheath whatever. The synopsis of genera will then be as follows:

I. No horns in the male.

Molars brachyodont..... ....*Palæomeryx*† Von Meyer.

* Leidy, Cope; Procervulus Gaudry.

† Should *P. eminens*, type of Palæomeryx, have possessed horns, as suspected by Schlosser, the generic name must take the place of Dicrocerus below, and be replaced by one of the various names which apply to hornless species.

II. Horns covered with skin (Cosorycinæ).

Teeth brachyodont; no frontal excrescence.....*Blastomeryx* Cope.

Teeth prismatic; no frontal excrescence.....*Cosoryx* Leidy.

III. Horns naked (Sivatheriinæ).

Teeth brachyodont; two pairs of horns, all separate
Sivatherium Cautl. Falc.

Teeth brachyodont; two pairs of horns; those of the anterior pair from a common base.....*Bramatherium* Cautl. Falc.

Teeth brachyodont; one pair of horns, from a single base
Hydaspitherium Lydd.

Teeth brachyodont; one pair of horns, from distinct bases
Dicrocerus Lart.

IV. Horns covered with a horny sheath; teeth hypsodont (Bovinæ).

a. No internal column of true molars.

β. No lateral ungues. (Nasal bones normal; postzygapophyses single.)

Horn-sheath furcate..... *Antilocapra* Ord.

Horn-sheath simple.....*Nanotragus* Sund.

$\beta\beta$. Lateral ungues present.

γ. Nasal bones separated from maxillary and lachrymal bones.

Horns simple, one pair.....*Sæga* Gray.

$\gamma\gamma$. Nasal bones more or less in contact with lachrymal or maxillary bones.

δ. Posterior postzygapophyses single. (Numerous species not examined.)

ε. Inferior premolars three.

Horns one pair.....*Antidorcas* Gray.

$\varepsilon\varepsilon$. Inferior premolars four.

Horns two pair.....*Tetracerus* H. Smith.

Horns one pair; last inferior molar with four columns..*Neotragus** Gray.

Horns one pair; last inferior molar with five columns....*Ovis*† H. Smith.

$\delta\delta$. Posterior postzygapophyses double.

Horns one pair; inf. mol. 3 with five columns.....*Capra* Linn.

aa. One or more superior true molars with a median internal column.

Dorsal postzygapophyses single.....*Ægocerus*‡ H. Sm.

Dorsal postzygapophyses double.....*Bos*‖ Linn.

A great number of names have been given to groups of species of the Bovinæ, especially within the limits of the genus Ovis of H. Smith. Here the various forms of sheep and antelopes have been distinguished

* *N. saltianus* type. This character is derived from authority to which I cannot now refer. I have not seen it.

† Includes the following supposed genera: Autilope, Gazella, Cervicapra, Oreotragus, Cephalophus, Strepsicerus, Damalis, Alcelaphus, Nemorrhædus, Rapicapra, Caloblepas, Haplocerus, Ovibos, Ovis, and Anoa.

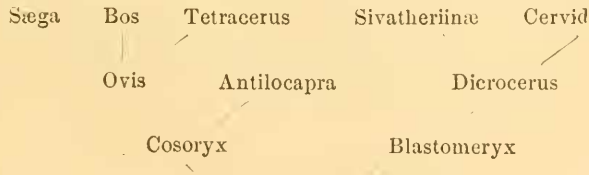
‡ Includes the following supposed genera: Eleotragus, Ægocerus, Oryx, Addax and Portax.

‖ In *Bos americanus* the postzygapophyses are single except on the last lumbar.

as genera and named accordingly. So far as concerns the skeleton, further subdivisions than those indicated in the above table do not appear to exist, and none have been pointed out. The divisions proposed appear to be rather those of one extensive genus. The modifications of the skull have reference to the position of the horns. These are processes of the frontal bones, and are placed at points from above the eye to the posterior angle of the facial plane of the skull. In the latter case this angle approaches very near to the supraoccipital crest or inion, and the parietal bone is reduced to an exceedingly narrow band between the frontal and occipital bones (Rütimeyer).* Forms with anterior horns and well-developed parietal bone are *Ovis gazella* and *Tetracerus quadricornis*, while the *Ovis gnu* displays the parietal extremely reduced, and become chiefly lateral in position. As regards the forms of the horns themselves, they present no important differences, but are angular and revolute in the section Ovis, and cylindric in the division Antilope. In the latter they vary in direction from straight to spiral or curved in different directions. Within the genus Ovis the end of the muzzle is naked or hairy, the latter in the typical forms and in those inhabiting northern and alpine localities generally. Those species that inhabit grassy or desert plains have the end of the nose naked.

Within the genus Bos modifications are observed parallel to those in the genus Ovis. The frontal bones with the horn processes are produced more and more posteriorly until the parietal bones are reduced to a narrow band across the posterior part of the skull. The bisons have the horns most anterior; then follow the buffalos, and the extreme is reached in the true oxen, of which the domesticated animal is the type.

The following table will give an idea of the phylogeny of the Bovidæ:



The hornless Palæomeryx has given origin to the horned Boöïdea; on the one hand to the brachyodont (Blastomeryx, etc.), and on the other to the hypsodonts (Cosoryx, etc.). A cornification of the integument in a fork horned Cosoryx produced Antilocapra, while the same process in a simple-horned Cosoryx produced Ovis. The development of this type has undergone the three principal modifications indicated by the three genera which succeed upwards. In Sæga an extraordinary development of the muzzle takes place, which causes a change in the relations of the nasal bones. In Tetracerus another pair of horns is developed in front of

* Die Rinder der Tertiär-Epoche; Abh. Schweiz. Pal. Gess., v, 1878.

the usual pair. Bos develops complications of the molar teeth in both jaws.

On the brachyodont side the development of the dermal covering of the horns of Blastomeryx is arrested, and naked horned types follow. In the Sivatheriine group no further change follows except complication of the horns. In the Cervine group, on the contrary, the habit of shedding them becomes fixed, and a new family has its origin.*

Of the CERVIDÆ or the Boöïdea which shed their horns, the genus Cervus is one of the earliest with which we are acquainted. Undoubted species of the genus occur in the Pliocene, and Upper Miocene species are also referred to it. As species from the Lower Pliocene (*C. matheroni* Gerv.) are referred to Capreolus, those of the Miocene may not be true Cervi. Their structure is not sufficiently known to determine this point. The arrangement of the genera is as follows. The three primary divisions were established by Brooke.

I. Lateral metapodials complete only distally, and supporting deer claws (Telemetacarpi).

a. Nasal passages posteriorly two, separated by vomer (Cariaci)

Horns simple spikes.....*Coassus* Gray.
Horns more or less furcate.....*Cariacus* Gray.
Horns palmate.....*Rangifer* H. Smith

aa. Nasal passage posteriorly one, not divided (Capreoli).

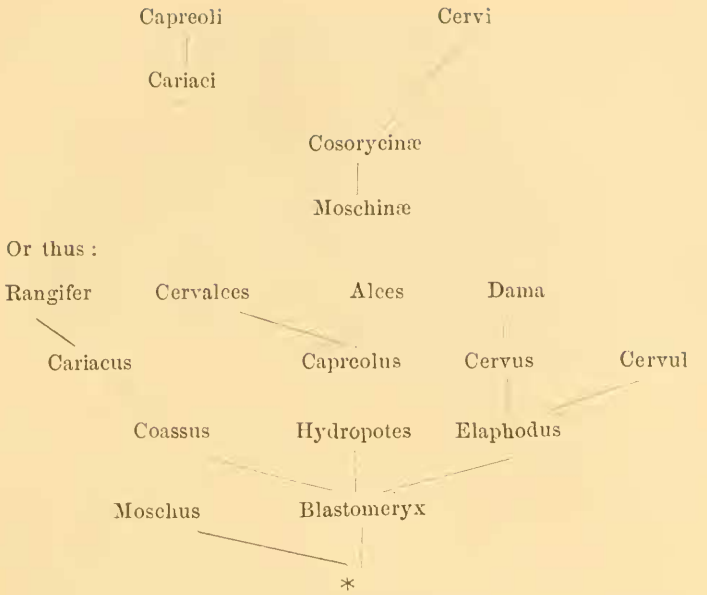
No horns.....*Hydropotes* Swinh.
Horns furcate; no postantler.....*Capreolus* Gray.
Horns palmate; no postantler.....*Alces* H. Smith.
Horns palmate; a postantler.....*Cervalces* Scott.

II. Lateral metapodials represented by proximal splints only; nasal passage not divided (Plesiometacarpi). (Cervi.)

Frontal cutaneous glands; horns furcate.....*Cervulus* Blv.
No frontal glands; horns simple.....*Elaphodus* M. Edw
No frontal glands; horns furcate.....*Cervus* Linn.
No frontal glands; horns palmate.....*Dama* H. Smith.
Horns furcate; brow antler greatly exceeding beam, (Gill)
Elaphurus M. Edw.

The phylogeny of these genera cannot be fully known until the skeletons of the extinct genera and species have been obtained. It is, however, certain that the short series of genera included in each of the three divisions (II *a* and *aa*, and III), are genetic series; and also that division I is ancestral to both II and III, although perhaps by an extinct genus differing in some respects from Moschus. These relations can be thus expressed:

* I have described the probable mode of origin of the deciduous horns of the deer in Report U. S. G. Survey, W. of 100th Merid., iv, p. 348, 1877.



Each of the genetic series commences with a genus with no or very simple horns. The next genus or stage presents branched horns, sometimes of great complexity. The last term in each is the palmate horn, where a greater or less number of the tines unite to form a plate. These series, as is well known, correspond with the history of the growth of the horns in successive years of the life of each species.

None of the genera of this family are extinct except Cervalces Scott.

The following series may approximate a correct representation of the phylogeny of the genus Bos, expressed in genera.

Bos Ovis (sens. lat.) Cosoryx Palæomeryx	Bovidæ.
Dremotherium	Moschidæ.
Amphitragulus Gelocus Leptomeryx Dorcatherium	Tragulidæ.
*	
Anthracotherium Cebochœrus	Anthracotheriidæ.
*	
Pantolestes	Pantolestidæ.

In conclusion I would remark the fact that the gradual approaches in character to the Bovidæ by the recent and extinct genera and families, furnishes one of the most admirable illustrations of the law of progressive specialization by evolution known to me.

Note.—Professor Gill has presented in his system of the Mammalia some reasons why the Suidæ should be more exactly defined than I have given above. In the Suinæ and Phaochœrinæ the postglenoid process is wanting or rudimental, and the mandibular condyle is flat and triangular. In the Dicotylinæ and Hippopotaminæ the postglenoid process is well developed and the condyle is subcylindric, as is also the case in Elotherium. I therefore place the two subfamilies named in a family separate from the Suidæ, under the name Hippopotamidæ, to which it is possible that Elotherium should be united as a third subfamily.

Biographical Notice of Isaac Lea, LL.D. By Joseph Leidy, M.D., LL.D.

(*Read before the American Philosophical Society, November 18, 1887.*)

In accordance with the custom of this Society, which requires that a record shall be made of the claims of its deceased members to remembrance, at the request of our President, I have prepared a brief sketch of one who was distinguished among us, our late much respected fellow-citizen and friend, Isaac Lea, LL.D. A more detailed memoir than the one I offer seemed supererogatory from the fact that only a short time previous to his death, there was published in the Bulletins of the United States National Museum, a volume containing a Biographical Sketch of Mr. Lea, comprising fifty-nine pages ; and a Bibliography of his publications with a synopsis of the material therein contained, comprising 278 pages, prepared at the request of the Smithsonian Institution, by Mr. N. P. Scudder. To this source I have conveniently applied for much of the information of my notice.

Isaac Lea was born March 4th, 1792, in Wilmington, Delaware. His grandparents, John and Hannah Lea, came from Gloucestershire, England, and accompanied William Penn in his second visit to this country. They were members of the Society of Friends, among whom they were noted as ministers. The father, James Lea, was a merchant, and at the age of fifteen Isaac went to Philadelphia to engage in a similar pursuit. In 1814, the country being at war with England, Isaac joined a volunteer rifle company, which offered its services to the Governor of the State in case of need. As the services were not required, the company was soon disbanded ; but in consequence of Isaac joining it, he lost his birthright in the Society of Friends.

At an early age Isaac showed a love for natural history, in which he was encouraged by his mother, who was herself fond of botany, and in-